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Larval Growth and Development of the Japanese Toad, *Bufo bufo formosus*, at Iwakura, Kyoto

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Abstract

Yearly differences in the growth and development of the larval Japanese common toad, *Bufo bufo formosus*, growing in temporary pools in a swamp at Iwakura, Kyoto, were compared for the 1977 and 1978 seasons. Tadpoles showed more rapid development in 1978 than in 1977 due to a more delayed breeding season and subsequent higher water temperature in 1978. However, development of the 1978 larvae was retarded in the later period, resulting in similar embryonic and larval periods of 58–60 days in both years. Developmental retardation in 1978 was assumed to be the result of density effect. Tadpoles in 1977 had larger body sizes than those in 1978, especially in body weights, and such differences were presumed to be caused by a differential population density. Tadpoles delayed in development tended to have smaller body sizes than those reached at the same developmental stage earlier. Body proportions showed small yearly differences compared with absolute measurements, and were almost constant from Stages 31 to 39. This tendency indicates that body proportions are of value for systematic work. Larval survival at Iwakura was briefly noted: a female toad spawns ca. 5,000 eggs, the average hatching rate being about 90.2%, and 5.5–20.2% of hatched embryos are assumed to complete metamorphosis. Whether the observed difference in metamorphic rates has significance is yet to be clarified.

Introduction

Tables of normal developmental stages, establishing a basis for comparing and describing anuran embryos and larvae, have been made by many authors since the end of the last century. LIMBAUGH and VOLPE (1957) made a complete table of normal developmental stages from fertilization to metamorphosis for *Bufo valliceps*, and, later, GOSNER (1960) modified it for other anuran species. These tables are currently used in various fields of anuran biology (e.g. BEISWENGER, 1978; GAUDIN, 1978; DUELLMAN and TOFT, 1979).

It has rarely been examined, however, whether or not developmental patterns of tadpoles grown under natural conditions completely fit these laboratory-made tables. Moreover, the ranges of variation both in rates of development and in the morphometrics of a given stage, have been inadequately investigated in tadpoles of the same species grown under different conditions.

The Japanese common toad, *Bufo bufo formosus*, deposits eggs in various bodies of still water, such as ponds, pools, ditches, and rice fields (MATSUI, 1975); at Iwakura, where the present investigation was performed, toads breed in temporary pools in the marsh. Different breeding seasons resulted from yearly meteorological fluctuations.

The subsequent larval periods provided these annual populations with different growing conditions. The purpose of this study is to describe and compare the growth and developmental patterns of the larvae of the Japanese common toad from a restricted breeding site over a two year period.

Samples and observations were made at Iwakura in 1977 and 1978. Yearly differences in the rates of development and in the growth patterns were investigated. Along with the absolute measurements of body parts, some body proportions were determined to reexamine LIMBAUGH and VOLPE's statement, "relative body proportions are constant during the greater part of development" (LIMBAUGH and VOLPE, 1957: 25). Further, the problems of larval survival, which are regarded to have basic importance for anuran demographic studies (TURNER, 1962), were preliminarily referred to in the present study.

Study Area and Methods of Observation

Iwakura is situated in the northern suburbs of the city of Kyoto. The study site is a swamp at the foot of low mountains, bordered by rice fields in the south, and is at an elevation of about 170 m. The surrounding low mountains are covered by deciduous broadleaf trees. The swamp is covered by grasses, and several alder trees. *Bufo bufo formosus* usually lays its eggs in late March to early April. Breeding occurs within a short period of one to two nights.

Sampling was made once a week from 12 April to 24 May in 1977, and from 1 May to 12 June in 1978. The number of sampled tadpoles is summarized in Table 3. In 1978, tadpoles were collected from three narrowly disjunct localities, but these samples were measured together. Within 24 hours after collection, the live animals were weighed with a Sartorius balance, Model 1205 MP to an accuracy of 1 mg. Prior to weighing, the tadpoles were blotted on paper towels. After weighing, the animals were fixed in 15% commercial formalin, and measurements on total length (TL), snout-vent length (SVL), tail length (Tail L), and maximum tail height (Tail H) were made. Small larvae were measured under a binocular dissecting microscope equipped with an ocular micrometer. Large animals were measured with a vernier caliper, to an accuracy of 0.05 mm. All specimens were examined with a binocular dissecting microscope to determine the developmental stages (St.) established by LIMBAUGH and VOLPE (1957). The discrepancies in applying this table to the larval Japanese common toad will be discussed later. The table was adequate for our materials, but our determination was made on the condition of limb buds. For analyzing the body proportions, 100 Tail L/SVL, 100 Tail H/SVL, and 100 Tail L/Tail H ratios were calculated.

The results of the measurements and the calculated body proportions were analyzed in the following two categories: 1) samples gathered together by date regardless of their developmental stages, and 2) samples belonging to the same developmental stage regardless of the sampling date. Student's *t* tests were performed on the 1977 and 1978 series for the two categories mentioned above. In the comparisons of the

first category, tadpoles of nearly the same age, e.g. 15th day in 1977 and 16th day in 1978, were compared. In order to determine if the values of the proportions were constant, statistical comparisons were performed for each proportion value among some stages of each year.

In the later descriptions, the embryonic and larval periods were divided into three time portions of unequal length: early (0–20 days), middle (21–40 days) and late (41–60 days). Also, developmental stages were divided into four periods according to MUTO et al. (1968): embryonic (St. 1–22), early larval (St. 23–24), middle larval (St. 25–41) and late larval (St. 42–46) stages.

The temperatures of the air, water, and ground were recorded on every occasion. In order to determine the daily fluctuation of temperatures, recordings were made at five different times of day: 0700 h, 0800 h, 1300 h, 1800 h, and 1900 h, on the 15th, 36th, and 57th day after oviposition in 1977. In addition, temperatures in the aggregation of tadpoles were recorded whenever possible.

Results

Changes in Microhabitats

The locations and the sizes of the swamp pools where these tadpoles grew changed during the observation periods. Generally the water volume decreased with time.

Toads spawned one cluster in the swamp pool and two in the pool on the path adjacent to the swamp on 29 March 1977. On 12 April, however, the eggs in the pool on the path were lost for unknown reasons. Consequently, only one cluster remained in the swamp. The size of the initial pool on 12 April was 3.8 m². The final size at the time of metamorphosis was 0.07 m² on 20 May, 1.9% of the initial size.

The initial range in which eggs were deposited was 6.91 m² in total on 1 May 1978. Later, parts of water range were dried up. Thus the final range at metamorphosis was 0.26 m² on 31 May, 3.8% of the initial size.

The water range occupied by tadpoles in 1978 was larger (1.8 times initially and 3.7 times finally) than in 1977.

The results of temperature recordings are summarized in Table 1, and those made at an interval of three weeks in 1977 are shown in Fig. 1. Although temperatures fluctuated according to weather conditions, all three recordings of air, water, and ground temperatures showed generally higher values in the daytime. As is evident from the evening recordings, temperatures steadily increased as time advanced.

The water temperatures, recorded in 1978, cannot be directly compared with those recorded in 1977, because of the differences in the time when records were made. The 1978 records, however, seem to be slightly higher than corresponding 1977 records when they are fitted into daily fluctuation curves estimated from Fig. 1.

From early to midday, eggs and tadpoles got direct sunlight, but the rapid growth of grasses gradually covered the water surface and prevented sunlight from reaching the tadpoles.

Temperature in the aggregation of tadpoles was measured and compared with

the nearby water temperatures (Table 2). Although the data are meager and variable, a marked increase in temperature was evident when tadpoles were found aggregated under direct sun (10 May 1977).

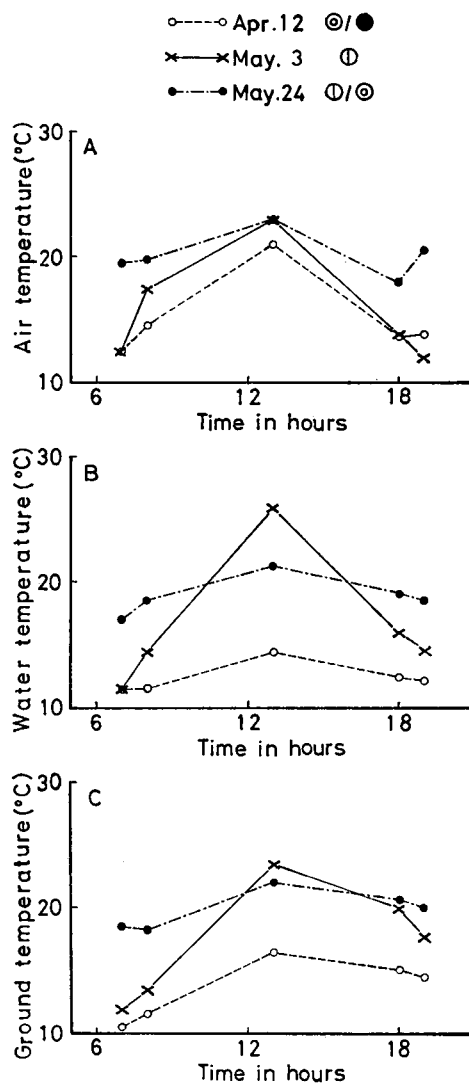


Fig. 1. Daily fluctuations of temperature measurements showing the result in 12 April (open circle), in 3 May (cross), and in 24 May (solid circle), 1977.

Larval Survival

From counts on egg masses laid by females taken to the laboratory, the female toads from Iwakura spawn about 5,000 eggs per individual. Sections of several egg masses were sampled a few days after they were laid at the study site, and were taken to laboratory for a determination of the actual hatching rate. The average hatching

Table 1. Water temperatures in 1977 and 1978, paired by the age of tadpoles after oviposition.

Age in Days		1977			1978		
'77,	'78	Date	Time	W.T. (°C)	Date	Time	W.T. (°C)
1,	1	Mar. 29	11:30*	18.5	Apr. 17	12:30**	16.5
15,	16	Apr. 12	13:00***	14.5	May 1	15:00**	22.9
22,	23	Apr. 19	12:00**	14.0	May 8	16:30**	18.4
29,	30	Apr. 26	13:00**	21.0	May 15	17:00*	19.8
36,	37	May 3	13:00*	26.0	May 22	15:30**	16.3
43,	44	May 10	13:30*	25.5	May 29	16:00**	20.3
50		May 17	13:00*	21.5			
57		May 24	13:00**	21.3			

* Weather clear, ** cloudy and *** rainy.

rate, thus obtained, was 90.2% in 1977.

In 1977, only one of the three egg masses survived and metamorphosed. Therefore, the number of hatched tadpoles was presumed to be about 4,500. From this population, a total of 227 individuals were sampled before they began to metamorphose. At the time of metamorphosis, the pool was enclosed and the newly metamorphosed toadlets were counted and marked for future studies. The number of animals identified was 236. If we assume that the sampled individuals would have died in nature at the same rate as the remaining ones, about ten individuals of the sampled animals would have metamorphosed if they had not been killed. As a result, about 5.5% of hatched embryos were presumed to grow up to metamorphosed toadlets in 1977.

In 1978, some egg masses were laid close to one another so that the actual number was not known. There were at least four or five clusters. The population of tadpoles

Table 2. Temperature relationship between tadpole aggregations (T.T.) and water (W.T.). A.T. represents air temperature.

Date	Age in Days	Time	Temperature			
			T.T. (°C)	W.T. (°C)	Difference	A.T. (°C)
Apr. 12, '77	15	13:00***	16.5	14.5	+2.0	21.0
Apr. 26, '77	29	13:00**	20.5	21.0	-0.5	20.1
May 10, '77	43	13:30*	30.0	25.5	+4.5	26.5
May 17, '77	50	13:00*	22.0	21.5	+0.5	20.2
May 1, '78	16	15:00**	23.0	22.9	+0.1	27.0
May 8, '78	23	16:30**	18.3	18.4	-0.1	20.5
May 15, '78	30	17:00*	19.8	19.8	0	22.6
May 22, '78	37	15:30**	16.6	16.3	+0.3	18.5
May 29, '78	44	16:00**	20.9	20.3	+0.6	24.5

* Weather clear, ** cloudy and *** rainy.

was estimated to be comprised of ca. 20,000 individuals. Later, at least 1,857 tadpoles were identified as having died from desiccation, and 303 were sampled before metamorphosis occurred. Although the number of metamorphosed animals was numerous, most of them were captured in the enclosure and any escaped animals were considered to be few. Toadlets were taken to the laboratory for counting and marking. A total of 4,091 individuals was determined, but about a half of them died accidentally during handling. The survivors were returned to the study site and released. Theoretically, about 60 animals would have metamorphosed if they had not been sampled. Therefore, it is assumed that about 20.2% of hatched embryos grew up to metamorphose in 1978, far better than in 1977.

Metamorphosed toadlets dispersed rapidly and none were found a few days after release. Few young toads were found around the study site during summer season.

From field observations over a five year period, the number of adults participating in reproduction at the study site is confirmed to be less than 20 every year. The sex ratio in the breeding periods is disproportionate, the average male-female ratio being 5:1.

Development of Tadpoles

In 1977 eggs were laid on 29 March. Most of the larvae grew up to St. 45 on 23 May, and all metamorphosed by 27 May. Consequently, the larval period was about 60 days. In 1978 egg deposition was retarded; as the eggs were found to be at St. 14 on 17 April, it was assumed that they were laid on 16 April. On 5 June, tadpoles were at St. 43–45 and most metamorphosed by 12 June. Therefore, the larval period was

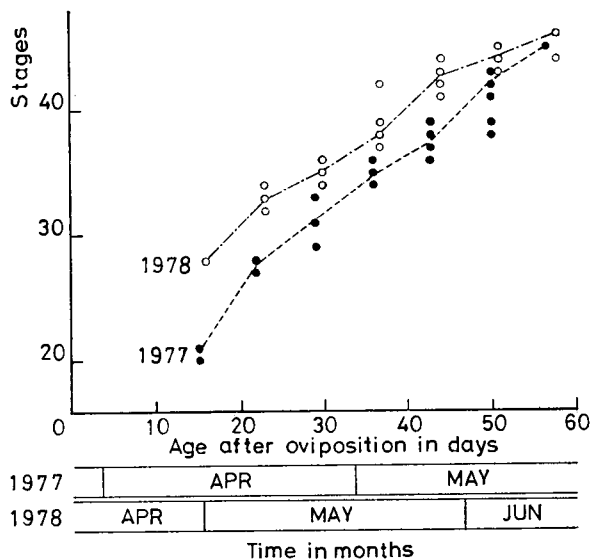


Fig. 2. Relationship between developmental stages and age after oviposition in days, showing actual stage in 1977 (solid circle) and 1978 (open circle). Lines connect mean stages.

about 58 days in 1978.

Developmental relationships among some characters in the Japanese toad differ from those in *Bufo valliceps* (LIMBAUGH and VOLPE, 1957), and our stage determinations were made principally by the length-diameter relationship of limb buds. In a few individuals, sequences in morphological changes were found variable: there was a tadpole with no metatarsal tubercles on its hindlimbs (St. 37, according to LIMBAUGH and VOLPE) but with a transparent cover over its forelimb (St. 41, according to the same authors); another individual had hindlimbs with only metatarsal tubercles and without pigment free patches (St. 38), but its forelimb already protruded (St. 42), etc.

The age after oviposition in days related to developmental stages is shown in Figure 2. In early days, the 1978 tadpoles showed a more rapid growth than the 1977 series. The developmental rates of the 1977 and 1978 series were comparable from

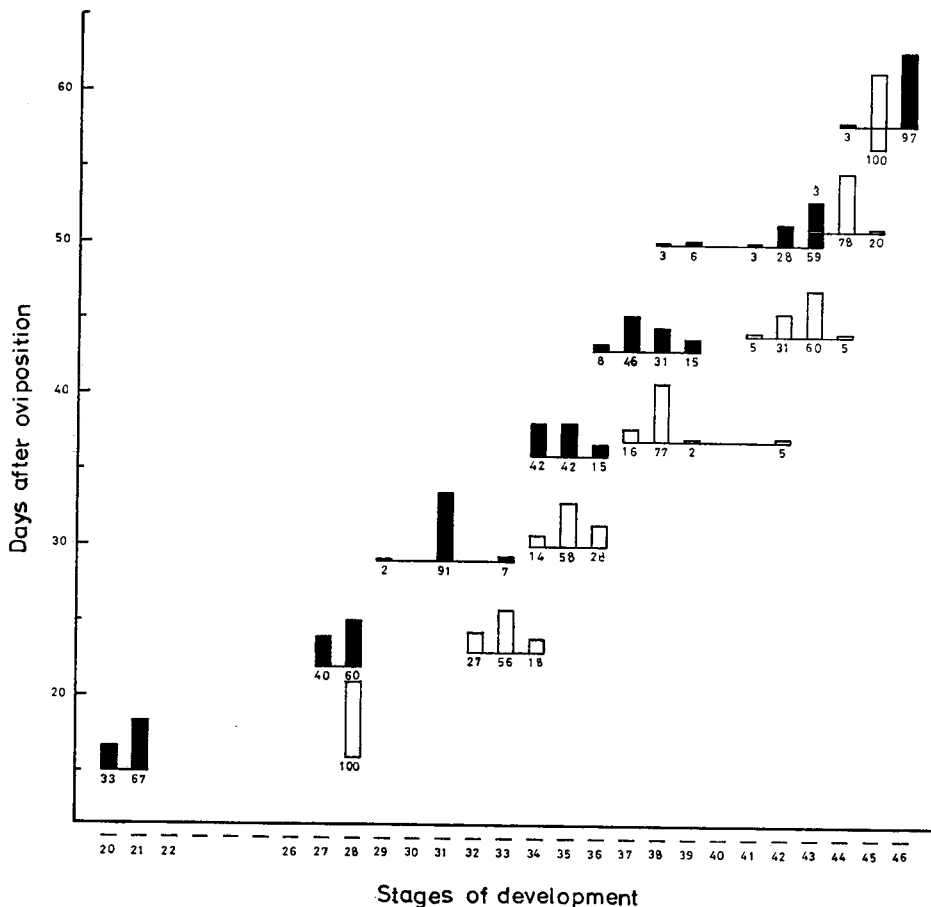


Fig. 3. Relationship between age after oviposition in days and developmental stages showing stage at age variations. The number beneath each bar represents the percentage of larvae that show the features of the stages at the age indicated. Solid rectangles indicate 1977 and open, 1978 samples. See text for notes on stages 23-25.

middle days to the beginning of late days. However, in the latter part of late days, the developmental rate of the 1978 series lessened. As a result, metamorphosis took place in almost the same length of days after oviposition in 1977 and 1978.

The differences in stages reached by similarly aged tadpoles, e.g. collected on 15th day in 1977 and 16th day in 1978, were checked statistically in the 1977 and 1978 series. There was a significant difference in all combinations.

Figure 3 shows the distribution of stages in each sampling. As is seen in the histogram, variation in the rate of development was not great except in a few cases (29th and 50th days in 1977 and 37th day in 1978), and at a given time, greater percentages of tadpoles were concentrated to a specific stage.

Growth of Tadpoles

(1) Samples gathered together by date

The 1977 and 1978 results gathered by sampling date showed curves crossing at

Table 3. Absolute measurements (means \pm SD, followed by ranges in parenthesis) of tadpoles gathered by collecting date.

Date	Age in Days	Stage	Sample Size	Weight (mg)	Total Length (mm)	Snout-Vent Length (mm)
Apr. 12, '77	15	20.7 \pm 0.5 (20-21)	33	13.3 \pm 2.3 (9-18)	10.8 \pm 1.3 (8.5-12.9)	5.6 \pm 0.3 (4.7-6.0)
May 1, '78	16	28	40	55.2 \pm 23.9 (40-87)	20.5 \pm 1.7 (16.7-23.9)	8.7 \pm 0.7 (7.6-10.3)
Apr. 19, '77	22	27.6 \pm 0.5 (27-28)	55	65.7 \pm 13.3 (27-94)	21.2 \pm 1.9 (15.3-24.6)	9.1 \pm 0.7 (7.2-10.5)
May 8, '78	23	32.9 \pm 0.7 (32-34)	45	103.6 \pm 24.9 (65-161)	24.3 \pm 2.2 (20.6-28.8)	10.2 \pm 0.8 (8.7-11.8)
Apr. 26, '77	29	31.1 \pm 0.6 (29-33)	46	120.6 \pm 13.8 (77-172)	26.3 \pm 1.7 (21.5-29.3)	10.4 \pm 0.6 (9.4-11.7)
May 15, '78	30	35.1 \pm 0.6 (34-36)	43	111.6 \pm 26.9 (73-162)	26.1 \pm 2.4 (21.4-30.7)	10.5 \pm 0.7 (9.1-11.9)
May 3, '77	36	34.7 \pm 0.7 (34-36)	33	156.2 \pm 24.8 (107-200)	28.5 \pm 1.7 (23.3-31.3)	11.4 \pm 0.8 (8.8-13.2)
May 22, '78	37	38.0 \pm 1.0 (37-42)	44	99.0 \pm 21.8 (55-145)	25.9 \pm 2.4 (19.2-31.2)	10.2 \pm 0.8 (8.0-11.8)
May 10, '77	43	37.5 \pm 0.9 (36-39)	26	144.1 \pm 20.8 (103-186)	28.4 \pm 2.1 (24.1-32.8)	10.9 \pm 0.7 (10.0-13.0)
May 29, '78	44	42.6 \pm 0.7 (41-44)	42	75.0 \pm 17.6 (45-106)	22.3 \pm 3.5 (9.9-27.0)	8.2 \pm 0.6 (7.2-9.1)
May 17, '77	50	42.3 \pm 1.3 (38-43)	32	132.3 \pm 32.6 (69-245)	26.9 \pm 3.3 (14.1-31.4)	9.4 \pm 0.6 (7.7-10.3)
Jun. 5, '78	51	44.2 \pm 0.4 (43-45)	40	56.8 \pm 15.0 (36-97)	9.2 \pm 0.9 (7.8-10.7)	8.1 \pm 0.6 (7.2-9.6)
May 23, 24, '77	56, 57	45	23	97.0 \pm 24.9 (46-136)	—	9.4 \pm 1.0 (7.0-11.5)
Jun. 12, '78	58	45.9 \pm 0.4 (44-46)	30	47.3 \pm 10.7 (24-64)	7.9 \pm 0.7 (6.0-9.1)	7.9 \pm 0.7 (6.0-9.1)

the point of the 29–30th day after egg-laying except for Tail H curves which have changing points at the 22–23rd day. The 1977 series is lower from the beginning to the changing points. This relationship reverses, thereafter, in all curves. Namely, growth in the 1977 series was worse at first, but, later became better than the 1978 series in every character examined (Table 3).

In 1977 the mean BW increased from the 15th to 36th day, and it decreased gradually thereafter until the 50th day. When metamorphosis occurred, it decreased rapidly. In 1978, it increased from the 16th to 30th day, and, thereafter, decreased until metamorphosis took place (Fig. 4). The maximum of mean BW, 156.2 mg, recorded on the 36th day in 1977, was 40.0% heavier than that of the 1978 series (111.6 mg, recorded on the 30th day) and their difference was significant ($t=5.42$, 33d.F., $p<.001$). Comparisons between presumably same age tadpoles of 1977 and 1978 resulted in significant differences in all cases except between the 29th day in 1977 and the 30th day in 1978 ($t=1.79$, 87d.F., $.1>p>.05$).

In 1977, mean TL increased rapidly until the 29th day and was almost constant

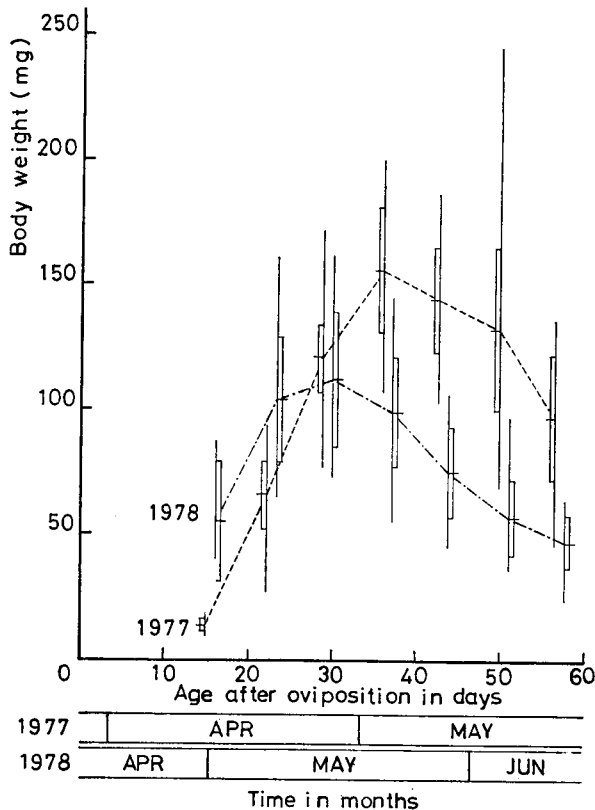


Fig. 4. Relationship between body weight and age after oviposition showing mean (horizontal line), range (vertical line) and standard deviation (open rectangle). Dashed line for 1977 and long-and-short dashed line for 1978.

thereafter; finally it rapidly began to decrease and equal SVL because of tail absorption. In 1978 it gradually increased till the 30th day and began to rapidly decrease on the 44th day (Fig. 5). The maximum value of mean TL, 28.4 mm, recorded on the 43rd day in 1977 was 8.8% larger than that of the 1978 series, 26.1 mm, recorded on the 30th day; the difference was significant ($t=4.10$, 67d.F., $p<.001$). The 1977 and 1978 tadpoles all significantly differed in TL except on the 29–30th day samples ($t=0.49$, 87d.F., $.7>p>.6$).

The mean SVL showed an increase until the beginning of middle days, followed by little increment thereafter. It decreased slightly at metamorphosis. Variation in this character was slight both in 1977 and 1978 samples (Fig. 6). The maximum value of mean SVL, 11.4 mm, recorded on day 36 in 1977 was 8.6% longer than that of the 1978 series, 10.5 mm, on day 30, and was significantly different from the latter ($t=4.83$, 74d.F., $p<.001$). Statistical comparisons between the 1977 and 1978 series gave significant differences except on day 29–30 ($t=0.46$, 87d.F., $.7>p>.6$).

The mean Tail L increased rapidly from the time of hatching, ceased to increase in the latter part of middle days, and quickly decreased as metamorphosis took place (Fig. 7). This measurement varied most at the time of metamorphosis. The maximum value of mean Tail L, 17.5 mm, attained on the 43rd to 50th days in 1977, was 11.5% longer than that in 1978, 15.7 mm, on the 37th day, and the difference was statistically significant ($t=4.07$, 100d.F., $p<.001$). The results of t tests for the 1977 and 1978 series were all significantly different from each other except on day 29–30 ($t=0.80$, 87d.F., $.5>p>.4$).

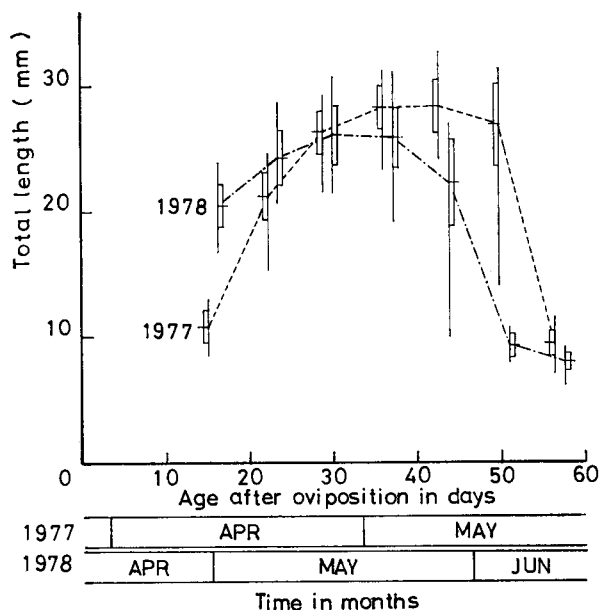


Fig. 5. Relationship between total length and age after oviposition in days; notation as in Fig. 4.

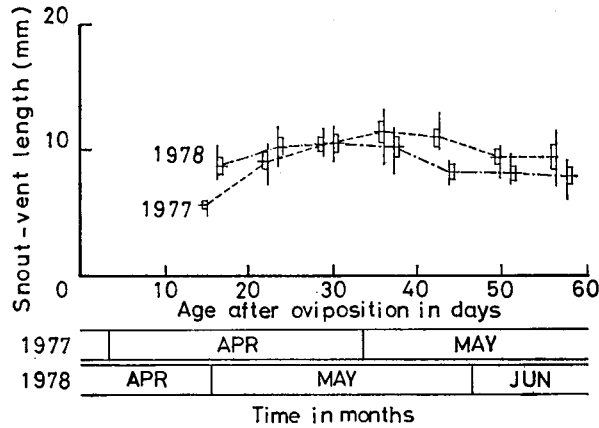


Fig. 6. Relationship between snout-vent length and age after oviposition in days; notation as in Fig. 4.

The maximum of mean Tail H, 5.2 mm, recorded on the 36th day in 1977, was 13.0% higher than that in 1978, 4.6 mm, recorded on the 30th day, and they were significantly different ($t=4.72$, 74d.F., $p<.001$). 1977 and 1978 series significantly differed except on day 22–23 samples ($t=0.25$, 98d.F., $.9>p>.8$).

(2) Samples gathered by stages

In general, 1977 tadpoles were larger in body size than the same staged 1978 tadpoles (Table 4).

As shown in Figure 9, mean BW fluctuated slightly both in 1977 and 1978, but, generally, it increased from the embryonic stages until St. 35–36. After, it decreased until metamorphosis. The maximum mean BW, 160.9 mg at St. 35 in 1977 was 30.0% heavier than that in 1978, 123.8 mg at St. 36; these values were different from each

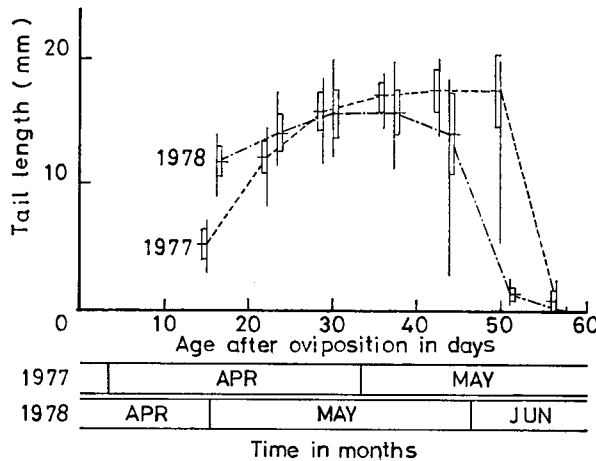


Fig. 7. Relationship between tail length and age after oviposition in days; notation as in Fig. 4.

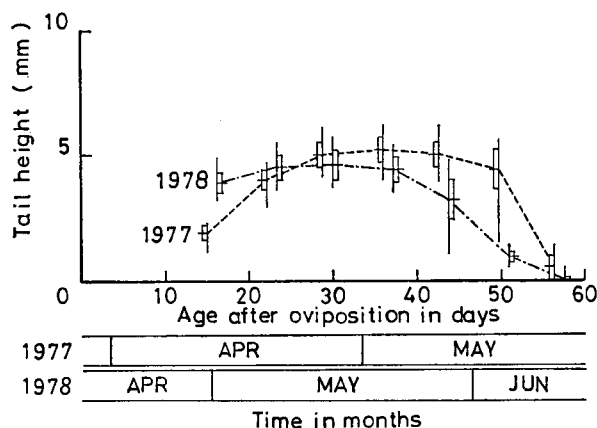


Fig. 8. Relationship between tail height and age after oviposition in days; notation as in Fig. 4.

other ($t=3.40$, 24d.F., $.01 > p > .001$). All comparisons of the 1977 and 1978 series resulted in significant differences except the St. 33 ($t=0.29$, 26d.F., $.8 > p > .7$) and St. 36 ($t=1.77$, 17d.F., $.1 > p > .05$) combinations.

Mean TL increased until the middle of middle larval stages, ceased to increase thereafter and finally decreased with metamorphosis (Fig. 10). The mean TL reached its maximum at St. 39 in 1977, 30.2 mm, and at St. 36 in 1978, 27.0 mm, the former being 11.0% longer than the latter and the difference being statistically significant ($t=2.46$, 16d.F., $.05 > p > .02$). In the comparisons of the 1977 and 1978 series, five out of ten differed significantly while the differences in the remaining five were statistic-

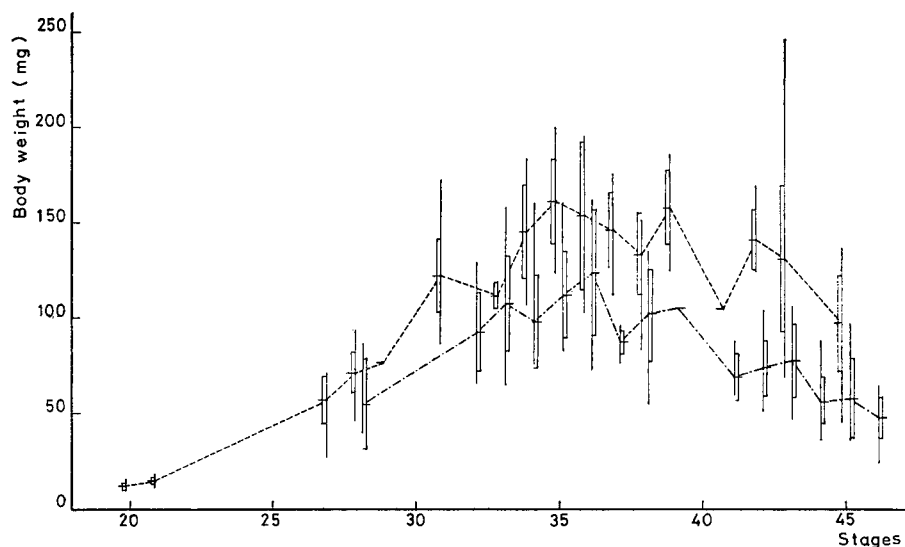


Fig. 9. Relationship between body weight and developmental stages; notation as in Fig. 4.

Table 4. Absolute measurements of tadpoles gathered by developmental stages.

Stage	Date	Age in Days	Sample Size	Weight (mg)	Total Length (mm)	Snout-Vent Length (mm)
20	Apr. 12, '77	15	11	11.4±2.0 (9-15)	9.5±1.0 (8.5-11.9)	5.5±0.3 (4.7-5.9)
21	Apr. 12, '77	15	22	14.3±1.8 (11-18)	11.5±0.7 (10.1-12.9)	5.6±0.3 (4.9-6.0)
27	Apr. 19, '77	22	22	57.1±12.4 (27-71)	19.7±1.7 (15.3-22.3)	8.6±0.6 (7.2-9.7)
28	Apr. 19, '77	22	33	71.4±10.7 (46-94)	21.6±3.6 (20.2-24.6)	9.5±0.4 (8.6-10.5)
	May 1, '78	16	40	55.2±23.9 (40-87)	20.5±1.7 (16.7-23.9)	8.7±0.7 (7.6-10.3)
29	Apr. 26, '77	29	1	76.8	21.5	9.8
31	Apr. 26, '77	29	42	122.2±19.3 (87-172)	26.4±1.6 (22.9-29.3)	10.4±0.5 (9.4-11.7)
32	May 8, '78	23	12	92.8±20.8 (66-129)	23.3±1.7 (20.6-25.4)	9.8±0.7 (8.9-10.9)
33	Apr. 26, '77	29	3	111.9 (105-119)	26.7 (25.8-27.2)	10.9 (10.4-11.2)
	May 8, '78	23	25	107.6±24.9 (65-158)	24.9±2.2 (21.2-28.8)	10.4±0.7 (8.7-11.7)
34	May 3, '77	36	14	145.3±24.5 (107-184)	27.4±1.8 (23.3-29.8)	11.1±1.0 (8.8-12.5)
	May 8, '78	23	14	98.1±24.3 (76-161)	23.9±2.2 (21.4-28.8)	10.0±0.8 (9.1-11.8)
	May 15, '78	30				
35	May 3, '77	36	14	160.9±22.2 (124-200)	28.8±1.3 (26.2-30.8)	11.4±0.5 (10.4-12.0)
	May 15, '78	30	25	112.0±22.6 (83-161)	26.2±2.0 (23.1-29.6)	10.6±0.6 (9.6-11.6)
36	May 3, '77	36	7	153.5±38.9 (103-195)	28.0±2.8 (24.3-31.3)	11.5±1.1 (10.0-13.2)
	May 10, '77	43				
	May 15, '78	30	12	123.8±33.0 (73-162)	27.0±2.9 (21.4-30.7)	10.7±0.9 (9.3-11.9)
37	May 10, '77	43	12	146.2±19.3 (112-176)	28.5±1.9 (24.1-31.4)	10.9±0.7 (10.1-11.9)
	May 22, '78	37	7	87.4±6.2 (76-96)	24.4±0.8 (23.6-25.5)	9.9±0.5 (9.4-10.9)
38	May 10, '77	43	9	133.6±21.1 (83-151)	27.5±2.4 (21.9-30.1)	10.6±1.2 (7.7-11.4)
	May 17, '77	50				
	May 22, '78	37	34	102.2±23.4 (55-145)	26.3±2.6 (19.2-31.2)	10.4±0.8 (8.0-11.8)
39	May 10, '77	43	6	157.7±19.6 (124-186)	30.2±1.6 (27.8-32.8)	10.9±1.4 (9.2-13.0)
	May 17, '77	50				
	May 22, '78	37	1	105	26.3	10.4
41	May 17, '77	50	1	104.8	25.3	9.0
	May 29, '78	44	2	69 (60-78)	22.7 (21.9-23.5)	8.0 (7.6-8.4)
42	May 17, '77	50	9	141.3±15.7 (124-169)	27.9±1.2 (26.3-29.9)	9.6±0.5 (9.0-10.3)
	May 22, '78	37	15	73.8±14.5 (51-104)	23.6±2.1 (20.6-27.0)	8.2±0.6 (7.4-9.1)
43	May 29, '78	44				
	May 17, '77	50	19	131.2±38.3 (69-245)	26.6±3.9 (14.1-31.4)	9.5±0.5 (8.8-10.2)
	May 29, '78	44	26	77.3±19.3 (47-106)	22.2±3.7 (9.2-25.4)	8.3±0.7 (7.0-9.3)
44	Jun. 5, '78	51				
	May 29, '78	44	34	56.0±13.7 (36-88)	9.3±0.9 (7.8-12.4)	8.0±0.6 (7.2-9.2)
	Jun. 5, '78	51				
	Jun. 12, '78	58				
45	May 23, 24, '77	56, 57	23	97.0±24.9 (46-136)	—	9.4±1.0 (7.0-11.5)
	Jun. 5, '78	51	8	57.8±21.0 (36-97)	9.2±0.9 (8.3-10.7)	8.3±0.9 (7.2-9.6)
46	Jun. 12, '78	58	29	47.6±10.8 (24-64)	—	7.9±0.7 (6.0-9.1)

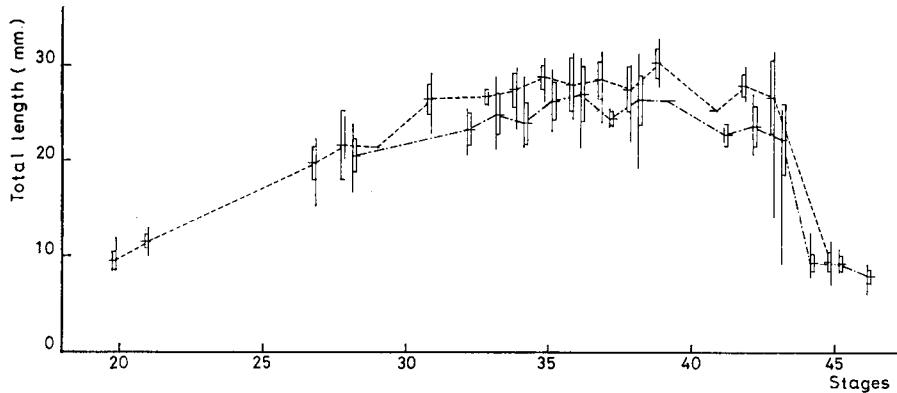


Fig. 10. Relationship between total length and developmental stages; notation as in Fig. 4.

ally insignificant ($p > .05$, in stages 28, 33, 36, 38, and 45).

The increase of mean SVL was small (Fig. 11). Its maximum was reached at St. 36 both in the 1977 and 1978 series: 11.5 mm and 10.7 mm, respectively; the difference was not significant ($t = 1.77$, 17d.F., $.1 > p > .05$). Three out of ten comparisons were not different between the two years ($p > .05$, in stages 33, 36 and 38), and 1977 tadpoles can be said to be larger than 1978 ones.

The mean Tail L increased from embryonic to the early two thirds of middle larval stages, ceased to increase thereafter, and decreased at St. 43 because of metamorphosis (Fig. 12). The maximum was reached at St. 39 in 1977 (19.3 mm) and at St. 36 in 1978 (16.3 mm), the former being 18.4% longer than the latter. These were significantly different from each other ($t = 3.18$, 16d.F., $.01 > p > .001$); the 1978 tadpoles had more continuously growing tails. Out of ten comparisons, four differed insignificantly between the 1977 and 1978 series ($p > .05$, in stages 33, 36, 38, and 45).

The mean Tail H showed a small increase both in 1977 and 1978 (Fig. 13). The maximum of mean Tail H was reached at St. 35 in 1977 and St. 36 in 1978, and the value, 5.3 mm, in the former was 10.4% higher than that in the latter, 4.8 mm. These were significantly different from each other ($t = 2.36$, 24d.F., $.05 > p > .02$). Out of ten comparisons, three were not different between 1977 and 1978 samples ($p > .2$, in stages 33, 36 and 45).

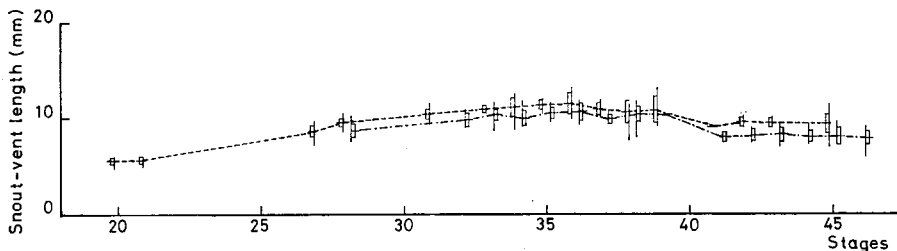


Fig. 11. Relationship between snout-vent length and developmental stages; notation as in Fig. 4.

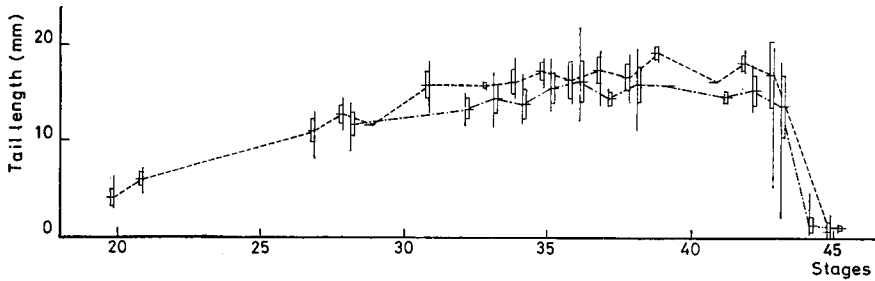


Fig. 12. Relationship between tail length and developmental stages; notation as in Fig. 4.

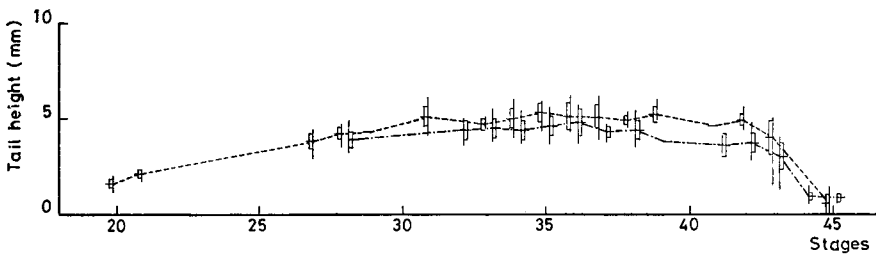


Fig. 13. Relationship between tail height and developmental stages; notation as in Fig. 4.

Body Proportion

As is shown in Fig. 14, the 100 Tail L/SVL values increased as the stage advanced, and they decreased with the beginning of metamorphosis because of tail absorption. The curves for 1977 and 1978 were similar. The maximum value was reached at St. 42 and that of 1977 approximated the 1978 series ($t=0.70$, 22d.F., $.5 > p > .4$). In

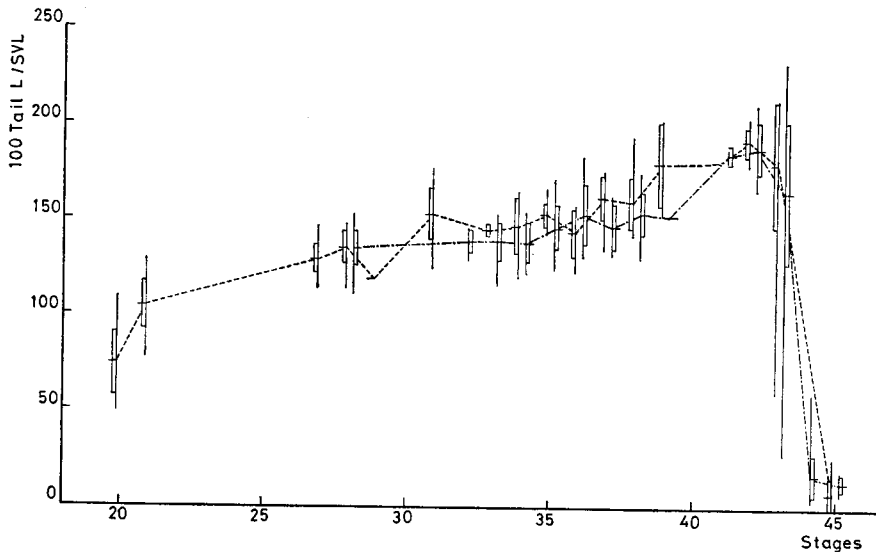


Fig. 14. Relationship between 100 Tail L/SVL and developmental stages; notation as in Fig. 4.

the statistical comparisons between the 1977 and 1978 series, this character showed all insignificant differences between the same stages except St. 37 ($t=2.80$, 17d.F., $.02 > p > .01$). Consequently Tail L relative to SVL does not differ markedly in a given stage according to year. In the comparisons between groups of tadpoles of neighbouring stages in each year, about half the combinations resulted insignificant differences ($p > .1$). In particular, during the middle part of middle larval stages, i.e. St. 31–39 in 1977 and St. 32–38 in 1978, tail length proportion values were similar between two neighbouring stage groups of tadpoles. Four out of seven (in 1977) and five out of six (in 1978) combinations resulted in insignificant differences ($p > .1$). This constancy held for the greater part of middle larval stages and no statistically significant differences were observed among tadpoles of the following stages: 31–35 and 37–38 in 1977; 32–34, 35–37 and 36–38 in 1978 ($p > .1$).

The 100 Tail H/SVL values are shown in Fig. 15. The mean values increased rapidly at first, stabilized during the late part of middle larval stages, increased slightly at the end, and then rapidly decreased at late stages because of tail absorption. The maximum of mean values was attained at St. 42 in 1977, and at St. 41 in 1978, the value in the former 13.7% larger than that of the latter. The difference was significant ($t=2.49$, 9d.F., $.05 > p > .02$). Out of ten comparisons between the 1977 and 1978 series, six differed significantly; the difference in the remaining four were insignificant ($p > .05$, in stages 28, 33, 34 and 36). Tadpoles in 1977 had slightly broader tail fins relative to SVL. In the comparisons between neighbouring stages eight out of ten combinations differed insignificantly both in 1977 and 1978 ($p > .05$). During St. 31–39 in 1977 and St. 32–38 in 1978, all combinations between neighbouring stages of larval groups were not significantly different ($p > .05$). Further, all combinations among stages did not differ significantly ($p > .05$, both in 1977 and in 1978), showing 100 Tail H/SVL values fairly constant during the middle part of middle larval stages.

The tail shape was expressed by 100 Tail L/Tail H ratio (Fig. 16); a low value

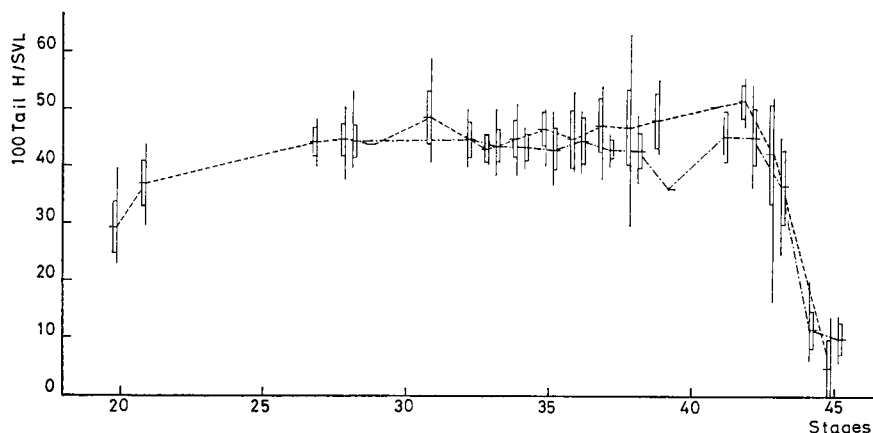


Fig. 15. Relationship between 100 Tail H/SVL and developmental stages; notation as in Fig. 4.

Table 5. Body proportions of the same stage tadpoles.

Stage	Date	Age in Days	Sample Size	100 Tail L/ SVL	100 Tail H/ SVL	100 Tail L/ Tail H
20	Apr. 12, '77	15	11	73.7 ± 16.5 (49.3 - 109.0)	29.2 ± 4.5 (22.9 - 39.5)	254.9 ± 60.4 (180.6 - 370.4)
21	Apr. 12, '77	15	22	104.4 ± 12.7 (76.5 - 129.0)	36.8 ± 3.9 (29.5 - 43.8)	284.9 ± 33.8 (224.9 - 345.6)
27	Apr. 19, '77	22	22	129.4 ± 7.6 (113.9 - 147.2)	44.2 ± 2.4 (40.0 - 48.4)	293.9 ± 20.4 (252.5 - 325.7)
28	Apr. 19, '77	22	33	135.3 ± 8.8 (113.8 - 148.4)	44.6 ± 2.8 (37.8 - 50.5)	304.6 ± 24.6 (238.5 - 354.3)
	May 1, '78	16	40	134.9 ± 9.4 (111.2 - 153.0)	44.4 ± 2.9 (39.9 - 53.3)	304.9 ± 23.7 (244.4 - 348.4)
29	Apr. 26, '77	29	1	118.9	43.9	270.9
31	Apr. 26, '77	29	42	153.2 ± 13.2 (124.5 - 177.0)	48.6 ± 4.7 (40.8 - 58.8)	317.0 ± 30.0 (236.4 - 365.5)
32	May 8, '78	23	12	138.7 ± 5.8 (128.9 - 146.3)	44.7 ± 3.2 (40.0 - 50.0)	311.2 ± 21.5 (284.0 - 352.9)
33	Apr. 26, '77	29	3	145.1 (142.9 - 148.1)	43.2 (40.6 - 45.7)	336.6 (315.8 - 351.6)
	May 8, '78	23	25	138.7 ± 9.8 (116.2 - 152.9)	43.5 ± 3.0 (38.6 - 50.0)	319.5 ± 21.1 (270.5 - 359.3)
34	May 3, '77	36	14	147.4 ± 14.2 (120.0 - 164.8)	44.9 ± 3.2 (38.6 - 50.9)	328.9 ± 35.3 (288.5 - 405.0)
	May 8, '78	23	14	138.2 ± 10.3 (121.7 - 153.7)	43.4 ± 2.5 (39.6 - 46.8)	319.0 ± 28.1 (280.0 - 374.4)
35	May 15, '78	30				
	May 3, '77	36	14	153.1 ± 6.3 (143.3 - 166.5)	46.6 ± 2.9 (40.1 - 50.0)	329.6 ± 24.9 (291.5 - 367.1)
	May 15, '78	30	25	146.3 ± 11.7 (123.7 - 172.4)	43.1 ± 3.7 (36.8 - 49.8)	340.5 ± 24.4 (288.3 - 395.5)
36	May 3, '77	36	7	143.7 ± 12.3 (122.7 - 157.5)	44.8 ± 5.1 (39.3 - 53.2)	323.1 ± 33.2 (290.7 - 387.0)
	May 10, '77	43				
	May 15, '78	30	12	153.3 ± 15.4 (131.4 - 182.9)	44.5 ± 4.1 (38.8 - 49.7)	345.6 ± 30.6 (298.1 - 409.5)
37	May 10, '77	43	12	162.3 ± 11.6 (134.6 - 175.7)	47.3 ± 4.7 (37.9 - 54.0)	346.1 ± 46.9 (296.8 - 464.1)
	May 22, '78	37	7	146.8 ± 11.7 (131.8 - 162.7)	43.1 ± 1.7 (40.0 - 45.7)	340.9 ± 29.5 (301.1 - 373.2)
38	May 10, '77	43	9	159.6 ± 13.2 (141.7 - 183.8)	46.8 ± 6.6 (39.6 - 63.0)	344.4 ± 34.3 (291.8 - 391.8)
	May 17, '77	50				
	May 22, '78	37	34	153.8 ± 11.3 (130.2 - 175.2)	42.8 ± 3.1 (37.1 - 48.8)	360.1 ± 29.4 (319.8 - 419.7)
39	May 10, '77	43	6	180.1 ± 22.1 (152.9 - 203.3)	48.0 ± 4.9 (42.2 - 55.2)	375.2 ± 26.6 (330.0 - 402.0)
	May 17, '77	50				
	May 22, '78	37	1	152.9	36.1	424.0
41	May 17, '77	50	1	181.1	50.6	358.2
	May 29, '78	44	2	184.5 (180.8 - 188.2)	45.3 (42.1 - 48.5)	409.9 (372.8 - 446.9)
42	May 17, '77	50	9	191.6 ± 7.5 (178.7 - 203.7)	51.5 ± 3.0 (47.0 - 55.6)	372.9 ± 23.1 (338.7 - 405.4)
	May 22, '78	37	15	188.1 ± 13.5 (165.9 - 211.1)	45.2 ± 4.9 (36.4 - 57.6)	424.0 ± 46.0 (303.2 - 489.1)
43	May 29, '78	44				
	May 17, '77	50	19	179.8 ± 33.0 (59.7 - 214.0)	42.3 ± 8.7 (16.5 - 52.0)	428.3 ± 50.8 (347.3 - 542.0)
	May 29, '78	44	26	165.2 ± 37.1 (27.9 - 232.9)	36.5 ± 6.5 (24.7 - 45.1)	459.4 ± 122.2 (165.4 - 943.6)
44	Jun. 5, '78	51				
	May 29, '78	44	34	16.7 ± 11.0 (3.4 - 60.4)	11.6 ± 3.3 (6.2 - 20.0)	96.3 ± 56.3 (36.7 - 310.0)
	Jun. 5, '78	51				
	Jun. 12, '78	58				
45	May 23, '77	56, 57	23(12)	7.5 ± 8.6 (0.0 - 25.5)	4.8 ± 4.9 (0.0 - 13.7)	157.1 ± 58.1 (66.7 - 264.7)
	Jun. 5, '78	51	8	13.4 ± 4.6 (7.3 - 18.6)	10.0 ± 2.7 (5.8 - 13.7)	78.2 ± 17.9 (58.3 - 116.7)
46	Jun. 12, '78	58	29	—	—	—

indicated high tail depth. The values were almost constant from the embryonic to a large part of the middle larval stages. The ratio increased thereafter until it rapidly decreased with the beginning of tail absorption. There was no marked difference between the 1977 and 1978 series. The maximum of mean values in 1977 was 7.3% smaller than in 1978 at St. 43, but the difference was insignificant ($t=1.04$, 43d.F., $.4 > p > .3$). In the comparisons between the 1977 and 1978 series, eight out of ten were statistically insignificant ($p > .1$), and the remaining two were significant at St. 42 and 45 ($.01 > p > .001$). In the comparisons between neighbouring stages nine out of ten and eight out of ten combinations did not significantly differ in 1977 and 1978

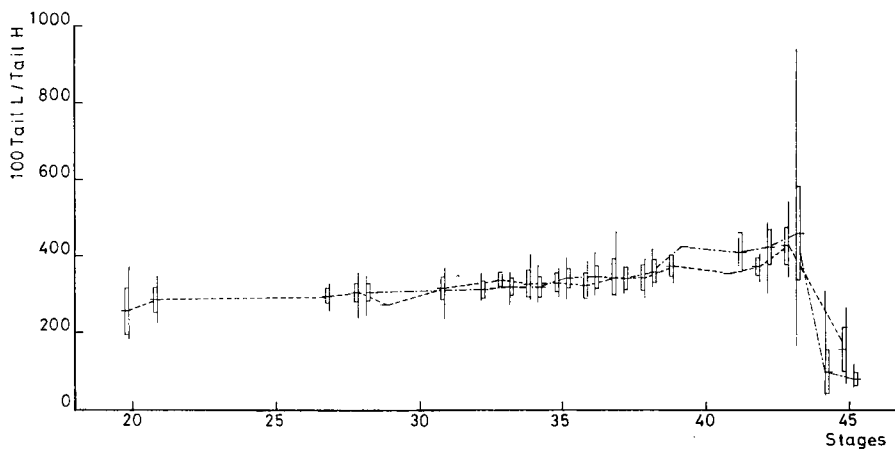


Fig. 16. Relationship between 100 Tail L/Tail H and developmental stages; notation as in Fig. 4.

($p > .05$), respectively. During the middle of middle larval stages, seven out of seven (1977) and five out of six (1978) combinations were insignificantly different ($p > .05$). The ratios were constant during St. 31–36, 33–38 and 37–39 in 1977 and St. 32–34, 35–37 and 36–38 in 1978. All combinations among these stages showed no significant differences ($p > .05$).

Discussion

Development

Developmental stages have been determined on the larval Japanese toads by several workers (OKADA and BABA, 1932; ICHIKAWA and TAHARA, 1966). MUTO et al. (1968) briefly reported the morphological deviation of the Japanese toad from *Bufo valliceps* (LIMBAUGH and VOLPE, 1957).

We have observed limb bud appearance before the disappearance of external gills as well as other peculiar developmental events in the Japanese toad. These findings are in agreement with those reported by MUTO et al. (op. cit.). LIMBAUGH and VOLPE's table was used, despite such discrepancies, since no serious problems were encountered in staging for the observed tadpoles.

Although no precise comparisons were made, stage variations in a given age tadpole from Iwakura did not differ greatly from those observed in the laboratory-reared *B. valliceps* (LIMBAUGH and VOLPE, 1957; Fig. 10). This tendency may suggest more uniform development of tadpoles under natural conditions than is generally expected.

The obvious differences between the 1977 and 1978 development rates for early days, i.e. faster embryonic development in 1978 than in 1977, are considered a result of late spawning in 1978. Temperatures in 1978 seemed to be slightly higher than those in 1977 in early days (Table 1). HERREID and KINNEY (1967) stated that the growth (=‘development’) rates of anuran larvae is determined by water temperature until larvae can swim freely. CALEF (1973) observed that the larvae of *Rana aurora* from three distinct areas of a lake had differential growth (=‘development’) rates owing to temperature differences and subsequent different hatching times.

During late days, the 1978 developmental rates decreased compared with early and middle days. Consequently the larvae of 1977 and 1978 completed metamorphosis in the same length of time. The 1978 temperatures were not markedly higher than the 1977 ones in the late days of larval growth. Therefore, the retardation in the 1978 series might not be attributed to the temperature being too high for their development.

HERREID and KINNEY (op. cit.) considered that environmental factors such as food and population density may determine the developmental rates of larvae in free-swimming stages in addition to temperature conditions. At Iwakura, neither quality nor quantity of foods were surveyed, but tadpoles were observed grazing humus and dead leaves at the bottom of pools.

Many students (ADOLPH, 1931a; 1931b; LYNN and EDELMAN, 1936; BROCKELMAN, 1969) considered that increasing density retards growth (exactly ‘development’) rates, decreases the size at metamorphosis, increases the length of larval period, and reduces the percentage of successful metamorphoses and survivorship. Moreover, RICHARDS (1962) reported the inhibition of larval growth (and ‘development’) by algae-like cells. We feel it necessary to investigate the existence and influence of the algae-like cells in the field. In 1978, tadpole density was about five times higher than in 1977. The prolongation of the 1978 series in late days may indicate the retardation of developmental rate and increase of larval period by density effect. The smaller body size at metamorphosis in 1978 than in 1977 seems to support these assumptions.

Growth

Smaller body size in 1977 tadpoles in early days compared with the same age 1978 tadpoles was apparently the result of younger stages in 1977 series. On the other hand, in the later part of middle to late days, the 1977 series showed larger body size despite their earlier developmental stages. This situation may reflect the effect of higher larval density, as mentioned above.

The curves gathered together by developmental stages moderately fluctuated, especially in BW and TL curves (Figs. 7 and 8), but such fluctuations were considered to be artifacts caused by small sample size in several stages. In addition, tadpoles of

a certain stage were gathered regardless of sampling date and, in reality, tadpoles whose development was delayed tended to have a smaller body size. This also seems to have contributed to the fluctuations.

Of the five dimensions measured, the body weight differed most markedly between 1977 and 1978 samples, the former being 1.5 times heavier than the latter on an average. Therefore the expected yearly differential conditions might be most clearly reflected by this dimension. Snout-vent length curves showed the least fluctuation in both years, making this character suitable for calculating body proportions.

The more continual tail length growth in 1978 than in 1977 is similar to BUSACK and ZUG's observation (BUSACK and ZUG, 1976). They observed differential tail length growth in two series of *Pelobates cultripipes* tadpoles collected from different habitats, and suggested that continual tail growth after body growth cessation was advantageous for maintaining high mobility during a highly vulnerable period.

The stage at which total length growth reaches its peak was determined in several toad species (LIMBAUGH and VOLPE, 1957; VOLPE and DOBIE, 1959; MUTO et al., 1968; MATSUI, 1976). The results obtained vary according to species, the stages ranging from 38 to 41. Our results showed that the stages, when dimensions reached their maxima, differed according to body parts even in samples collected in a year; the stage when one dimension reached its maximum differed annually. Further, fluctuations were considerable in every dimension. Therefore, it may be safely concluded that tadpoles grow up to maximum size at St. 36, somewhat earlier than other reports, and remain at about the same size until 39-40.

Body Proportion

LIMBAUGH and VOLPE (1957) found that the body proportions of *Bufo valliceps* remained constant during the greater part of larval development. In our results for 1977 and 1978, all three proportions calculated showed somewhat smaller differences than the actual measurements and scarcely fluctuated during St. 31-39. This result suggests that the body shape of tadpoles at Iwakura does not show marked variance, notwithstanding the yearly different conditions under which tadpoles grow, and that body proportions are reasonably stable during the greater part of middle stages (31-39). Therefore, ratios of some body parts in certain stages are considered to have some systematic value.

Larval Survival

The factors determining survival in anuran larvae are somewhat complicated: throughout the larval period meteorological catastrophes may injure larval populations, and severe temperature changes may reduce populations in early days; density and predation play an important role thereafter.

CALEF (1973) considered fungal infection, desiccation and freezing as the main causes of death of an embryo. HERREID and KINNEY (1966) noted lower fertilization success at low temperatures in the laboratory. There were little, if any, fungal infec-

tions and no desiccation at Iwakura during our investigation. Furthermore, neither freezing of embryos nor extreme low temperatures were observed, and no marked reduction in tadpole number occurred in early days.

Since the deposition sites at Iwakura are temporary pools in the marsh, eggs and larvae are susceptible to meteorological catastrophes. In fact, about 9% of the initial population was found desiccated in 1978. A similar phenomenon of population reduction by drying is reported for other anuran species that breed in temporary bodies of water (TURNER, 1962; KADEL, 1975), in contrast to those species breeding in permanent waters (CALEF, 1973). Yet, the survival rate in 1978 was higher than in 1977, showing little effect of drying on survivorship.

ADOLPH (1931a) pointed out that tadpoles in crowded cultures fed less readily than those in uncrowded ones. Tadpoles maintained on starvation diets, however, survived for many weeks, even though they did not grow (CALEF, 1973). Although our available data on food supply are limited, our casual field observations suggest tadpoles were well-fed. In fact, the more crowded 1978 tadpoles (15,700/m²; at metamorphosis in 1978, in contrast to 3,400/m²; in 1977) actually metamorphosed in higher percentages than the 1977 series after about the same length of larval period. Consequently, density effect, in respect to food supply, was considered to have little lethal effect on tadpole populations at Iwakura.

CALEF (1973) observed a rapid decline in number of tadpoles shortly after hatching and a less rapid decline thereafter until metamorphosis took place. A similar result was obtained by HERREID and KINNEY (1966). CALEF suggested that the reduction in mortality of later larval stages resulted from the larvae being too large for predators to eat.

A detailed survey on predators at Iwakura has not been made, but the newt, *Cynops pyrrhogaster*, which is regarded as a predator of toad larvae, inhabits this area. In addition, several *Natrix vivakari*, a small snake, were found swallowing large numbers of tadpoles on a few occasions. The pond skater, a possible insect predator, was seen in the pool. Whether or not predation was the most effective factor in reducing the number of observed populations remains to be determined.

The difference in the number of survivors completing metamorphosis seems large. It may possibly be within the range of population fluctuation. Long-termed observations are required for discussing population number.

The number of metamorphosed toadlets is much larger than the 20 reproducing toads which probably are composed of more than two age groups. These facts suggest remarkable mortality in toadlets before they attain sexual maturity.

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